Stone Boring Marine Bivalves from Monterey Bay, California

 \mathbf{BY}

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(1 Text figure)

INTRODUCTION

MONTEREY BAY HAS BEEN A CENTER for shell collecting by conchologists for more than a hundred years. Included in many of the early collections were representative bivalve borers of the families Mytilidae and Pholadidae, and Monterey Bay is the type locality for several species. SMITH & GORDON (1948) summarized these early studies and presented a list of all boring and nestling bivalves reported from Monterey Bay up to World War II. For many years after the Smith & Gordon paper appeared, little work was published on stone boring animals in Monterey Bay. In recent years, however, there has been renewed interest in this important group of animals and several theses and published papers have been partially or totally devoted to them (BOOTH, 1972; BURNETT, 1972; CLARK, 1978; DONAT, 1975; HADERLIE, 1976, 1977, 1979; HADERLIE & Donat, 1978; Haderlie et al., 1974; Minter, 1971).

Since 1970, a continuous long term study on marine bivalve stone borers by students and staff of the Naval Postgraduate School in Monterey has been underway. This study has consisted of two parts. First, the horizontal and bathymetric distribution and substrate preference of living borers within Monterey Bay have been investigated. This has involved extensive shore collecting, shallow water diving, and shipboard dredging operations. Second, experimental studies aimed at determining reproductive seasons, settling times, growth rates, and longevity of individual borers have been carried out. Studies have made use of experimental stone panels placed in the sea at various times and depths and for varying periods and then recovered and examined for evidence of bivalve borer settlement and growth.

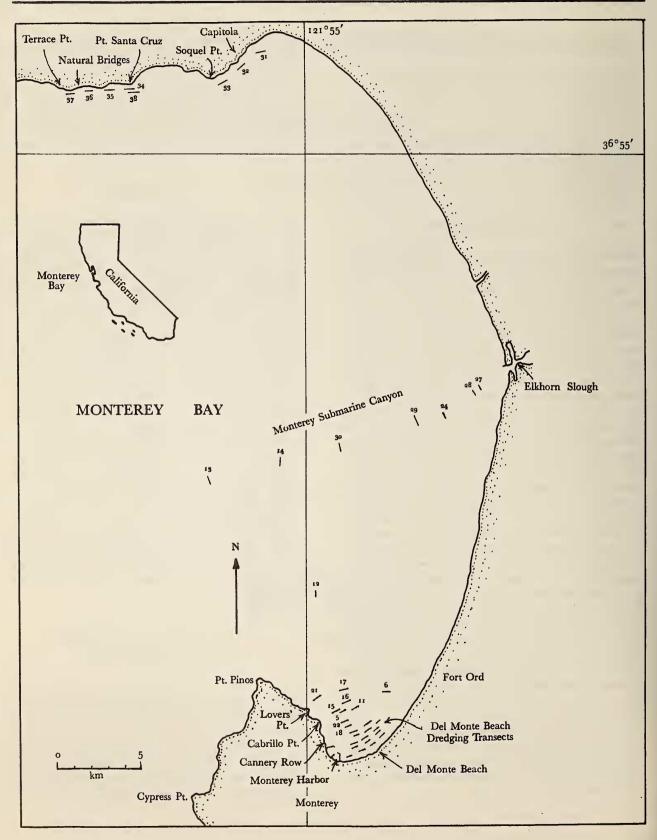
This paper presents the results to date of the first part of this study, namely the identity, distribution, abundance, and substrate preference of stone boring bivalves of the families Mytilidae and Pholadidae and associated nestlers in Monterey Bay.

ACKNOWLEDGMENTS

I want to acknowledge the help of many people, but especially Captain Reynolds and the crew of R/V Acania for their unfailing cooperation and help during many arduous hours of dredging operations over many years in all weather conditions on Monterey Bay. Also, I want to thank my colleagues and students who assisted in the hundreds of shallow water Scuba dives for making observations and collections, photography, or recovery of lost gear such as dredges. These include G. C. Booth, G. W. Clark, W. Donat, J. C Mellor, C. S. Minter, and J. Norton. In the early part of the study Dr. Ruth Turner of Harvard assisted in the identification of borers and has given advice on many phases of the work. Drs. R. S. Andrews and W. C. Thompson of the Naval Postgraduate School and Dr. H. G. Greene of the U.S. Geological Survey helped in sorting out the complex geology of Monterey Bay, and Florence Lee-Wong of the U.S. Geological Survey made the petrographic analyses of thin sections of various rock samples. The office of Naval Research, Oceanic Biology Program, has provided long term financial support for this project, and the Naval Postgraduate School Research Foundation Program has assisted in the intertidal part of the project.

TOPOGRAPHY AND GEOLOGY OF MONTEREY BAY

Monterey Bay is a large open embayment along the central California coast some 115 km south of San Francisco (see Figure 1). The mouth of the Bay is about 37 km in width when measured from Point Santa Cruz in the north to Point Pinos in the south. The shoreline at the southernmost part of the Bay, on the Monterey Peninsula, is a rocky headland composed of Santa Lucia granodiorite of Cretaceous age. From Monterey eastward and north to



Soquel Point there are broad sandy beaches backed by dune fields in the south and cliffs in the north. The shoreline in the vicinity of Santa Cruz is composed of steep bluffs with flat-topped terraces. These sea cliffs are Quaternary marine terrace deposits which overlie Pliocene Purisima Formation at Point Santa Cruz. This latter formation is exposed as yellow sandstone and siltstone in the intertidal zone. To the west of Point Santa Cruz the sea cliffs are composed of Pliocene Santa Cruz mudstone overlying layers of chert of Miocene Monterey Formation. This latter formation extends as broad terraces or finger reefs interspersed with sandy pockets into the intertidal and subtidal zones.

The subtidal topography and geology of Monterey Bay is diverse and complex. The sea bottom relief is dominated by the Monterey Submarine Canyon which originates less than 2 km west of Elkhorn Slough and extends westward for over 90 km as a deep, V-shaped cut in the continental shelf. The remainder of the Bay bottom is a relatively flat, gently sloping continental shelf, covered with unconsolidated sediments and interrupted by a few rocky reef outcrops. Galliher (1932) was the first to publish information on the location and lithologies of these rocky outcrops. SHEPARD & EMERY (1941), MARTIN (1964), and GREENE (1977) have extended these observations in many details and have also reviewed the extensive literature on the geology of Monterey Bay. During these previous studies, and from dredge hauls made during the present investigation, rock samples from many of these outcrops and from the walls of the Monterey Submarine Canyon have been obtained. Samples of porphyritic biotite granodiorite have been dredged from off Point Pinos and from the south wall of the Monterey Canyon. This granitic rock that forms the basis of the Monterey Peninsula is apparently also the dominant basement rock under Monterey Bay. The sedimentary rocks dredged from the bottom of the Bay are mudstones, siltstones, sandstones, cherts, and conglomerates derived from the Monterey Formation of middle Miocene age and from Pliocene Purisima Formation.

AREA of STUDY

This study has been limited to Monterey Bay which is here defined as the area to the east of a line running from Point

(← on facing page)

Figure 1

Map of Monterey Bay Area

Pinos on the Monterey Peninsula to Terrace Point west of Santa Cruz in the north. The area of most intense study, and that from which we have the most complete data, is the shallow subtidal zone off Del Monte Beach to the east of Monterey harbor at the most southerly end of Monterey Bay (Figure 1). This area is roughly defined by the extensive kelp bed made up primarily of Macrocystis pyrifera (Linnaeus, 1771) whose holdfasts are attached to the discontinuous outcrops of shale of the Monterey Formation. The water depth in the area of shale outcrops is from 10 to 20 m. In most of the area the bottom consists of relatively flat smooth shale, sometimes covered with sand to varying thickness, at other times completely exposed except for low lying sand pockets. In roughly the middle of the study site off Del Monte Beach, the topography is much more rugged with hummocks and ledges distributed parallel to the trend of the Tularcitos Fracture Zone which enters the Bay from the southeast. Some of these ledges are continuous ridges rising 2 m or more above the adjacent bottom and running several hundred meters seaward. The shale in this area has been examined and sampled repeatedly over the past 10 years by Scuba diving, and the benthic fauna and flora, including the distribution of several species of boring bivalves, have been investigated (BOOTH, 1972; BURNETT, 1972; HADERLIE, 1976; HADER-LIE et al., 1974; MINTER, 1971).

The present investigation has continued these studies and extended them seaward by using shipboard dredging techniques to sample the exposed shale in deeper water off Del Monte Beach and throughout Monterey Bay. Some dredge hauls were made in areas previously studied by shallow water diving in order to recover larger samples of rock substrate than can be collected conveniently by divers. During this investigation, we have successfully collected bottom samples on 40 dredge hauls in Monterey Bay (Figure 1).

In addition to the subtidal areas of Monterey Bay described above, we have surveyed the intertidal zones for sedimentary rocks which might harbor bivalve borers. At the southern end of Monterey Bay along the shore of the Monterey Peninsula only granitic rock is exposed in the intertidal zone and no bivalve borers can penetrate this hard basement material. From Monterey harbor around the Bay to Soquel Point in the north, the shore consists of sandy beaches. But from Soquel Point westward to Terrace Point, sedimentary rocks of both the Purisima Formation and the Monterey Formation are exposed in the intertidal zone as reefs or sea cliffs. We selected two of these reefs to the west of Point Santa Cruz for intensive study of bivalve borers.

METHODS AND EQUIPMENT

Our objectives in this study were to determine the identity, density of numbers of individuals, distribution horizontally and with depth, and substrate preference of mytilid and pholad borers in sedimentary rocks in and around Monterey Bay. As these borers are hidden, sometimes deeply, in the substrate, with only the distal ends of the siphons projecting out of the burrow, in order to find, identify, and count the borers it was usually necessary to mechanically break the rocks apart and remove the animals one at a time from their burrows. By removing and keeping representative living mytilid and pholad borers in sea water aquaria we were able to study the size, morphology, and color of the extended siphons after the animals had been positively identified using shell characteristics. With this information we were able, while diving in shallow water, to identify and quantify many of the bivalve borers found in the Monterey shale off Del Monte Beach. A photographic catalogue of typical siphons with the animals in situ in subtidal rock has been prepared (see BOOTH, 1972, HADERLIE et al., 1974, and MINTER, 1971, for details of techniques and representative photographs).

One major aim of this investigation was to sample sedimentary rock for borers in water below diving depths in Monterey Bay and to collect large rock samples from shallow water that were impossible to recover by diving. The Naval Postgraduate School's R/V Acania was used for most dredging operations using a heavy duty chain bag dredge with a mouth opening measuring 45 cm by 85 cm.

Attempts were made to locate and sample most of the sedimentary rock outcrops in Monterey Bay. In some cases specific areas were re-visited where earlier workers had recovered rock while dredging. This was particularly true of the dredging stations on the south wall of the Monterey Canyon. In other areas, such as in the shallow water off Del Monte Beach and off Santa Cruz, parallel tows were made through the kelp beds at progressively deeper locations. Beyond the kelp beds, where we had no idea if any solid substrate was exposed, random tows were made somewhat parallel to one another and running generally from southwest to northeast. In this way, a substantial part of the bottom was sampled particularly in the southern bight of the Bay south of 36°38′30″ N (a line running east from Point Pinos to Fort Ord).

After deciding on the specific locality to be sampled, the dredge was towed slowly over the substrate. If the behavior of the towing cable indicated that the dredge had been hitting solid substrate and breaking off pieces of rock so that the chain bag was full or nearly so, the dredge was recovered after having passed over 100 m or less of bot-

tom. In other cases the dredge was towed for up to 500 m, sometimes picking up rock at the very end of the tow, sometimes coming up empty. If the dredge collected a sample early in the tow it was recovered and then lowered again and the tow continued along the same transect. Thus, the samples of rock recovered came from various places along the transect, but we were never sure where the dredge actually collected the sample.

On the south wall of the Monterey Canyon the usual dredging technique was to position the ship over the deep part of the Canyon, lower the dredge to the bottom, then allow the ship to drift slowly south or east so that the dredge would be dragged upward over the wall to the edge of the shelf.

The location of various dredging transects is shown in Figure 1, and Table 1 lists the various dredging operations and the recovered samples. The position of the ship at the beginning and end of each transect was determined by visual bearings when close along shore or by Loran C when offshore. The depth of water and amount of dredging cable out was then used to estimate the path of the dredge along the bottom. This was then plotted on a standard No. 18685 (formerly C&GS No. 5403) chart of Monterey Bay. This chart with the plotted transects is on file in the Department of Oceanography, Naval Postgraduate School. In Figure 1, and in the location column of Table 1, only the general locality and water depth of the transects are given.

In order to learn more about the type of stone penetrated by borers, representative samples of bored sedimentary rock recovered during this study were analyzed by thin section to determine their petrographic nature. In addition, Clark (1978) subjected representative bored rock samples to carbonate analysis using a Leco W 12 Carbon Determinator (Model 761-100).

RESULTS

The following section will present results of (1) observations and collections made by shallow water diving on the

(adjacent column →)

Explanation of Table 1

In column Substrate Sample: Concr. = Concretions
In columns Relative Abundance, Vacant Bore Holes; and
Relative Abundance, Living Borers:

A = abundant F = few O = none

Table 1

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Monterey shale off Del Monte Beach, (2) dredging operations, (3) intertidal work near Santa Cruz, and (4) carbonate and petrographic analyses of representative rock samples.

Diving observations on Monterey Shale off Del Monte Beach

The paper by Haderlie et al. (1974) included a review of all diving operations and observations made in the kelp bed off Del Monte Beach up to that time. Since then, additional diving work has been done to sample parts of the exposed shale bottom that had not been examined previously. Methods and techniques employed were the same as in the earlier studies.

The following species of bivalve borers have been found while diving on the shale outcrops of the Monterey Formation off Del Monte Beach: Adula californiensis (Philippi, 1847), A. falcata (Gould, 1851), Litho phaga plumula Hanley, 1843, Barnea subtruncata Sowerby, 1846, Chaceia ovoidea (Gould, 1851), Netastoma rostrata (Valenciennes, 1846), Parapholas californica (Conrad, 1837), Penitella conradi Valenciennes, 1846, P. gabbii (Tryon, 1863), P. penita (Conrad, 1837) and Zirfaea pilsbryi Lowe, 1931. In addition the following molluscan nestlers have been found in vacant pholad holes: Crepidula perforans (Valenciennes, 1846), Hiatella arctica (Linnaeus, 1767), Irus lamellifer (Conrad, 1837), Kellia laperousii (Deshayes, 1839), and Petricola carditoides (Conrad, 1837). As will be pointed out below in the section on results from dredging, one additional species of pholad, Penitella fitchi Turner, 1955, was found in shale in slightly deeper water off Del Monte Beach.

Some of the borers listed above can readily be identified in situ by a diver, provided the animals are fairly large and the siphons are extended and exposed. These include Barnea subtruncata, Chaceia ovoidea, Parapholas californica, and Zirfaea pilsbryi. The siphons of all others are so small that, although they can be seen clearly projecting from a bored rock sample kept in an aquarium, they are exceedingly difficult to detect in the field under average diving conditions. The siphon tips of members of the genus Penitella can usually be distinguished from all other genera, but species determination in the field usually is impossible. Likewise, although the siphons of the mytilids Adula californiensis, A. falcata, and Lithophaga plumula are distinguishable from those of pholads, they are not sufficiently distinctive from species to species to allow for identification in the field.

Identification and attempts to quantify densities of populations of borers by observing the borers in place, while

diving, is further hampered by shifting sand at the Del Monte Beach diving site. Along this beach there is considerable onshore-offshore sand movement with seasons. Following the first storm waves striking the beach in November and December each year much of the sand is combed off the beach and distributed in subtidal waters out to about 10 m depth. Sand covers much of the flat shale outcrops, sometimes up to 30 cm or more in thickness, for several months of the year. Yet, as will be pointed out later, some of the bivalve borers in the shale survive this seasonal burial. Others that cannot tolerate periodic burial are limited in distribution to the projecting ledges and ridges that remain sand-free throughout the year.

As part of this over-all study, BOOTH (1972) attempted to determine the distribution and density of boring bivalves that could be identified in situ along two transects running seaward for 500 m off Del Monte Beach. He found a discontinuous distribution of species along each transect, and considerable variation between the transects. Booth noted that Parapholas and Zirfaea were best able to tolerate periodic sediment cover and that Chaceia was most commonly found boring horizontally into shale ledges. Additional diving operations since 1972 have confirmed these observations. Booth was unable to detect Adula, Barnea, Lithophaga, or Penitella species in the deeper water along the transects he studied and concluded these borers were restricted to shallow water. In other areas off Del Monte Beach, we have not only made observations while diving, but have recovered shale samples by excavating the substrate and have found representatives of all these genera except Barnea out to far beyond the ends of Booth's transects. Booth also concluded that variations in hardness and carbonate content of the exposed Monterey shale were the major factors influencing the inhomogeneous distribution of bivalve borers along his transects. However, recent dredging operations on the Del Monte Beach shale outcrops have allowed us to recover large blocks of Monterey Formation, particularly hard chert, and in this dense homogeneous rock we have found representatives of most of the genera of bivalve borers living side by side.

2. Dredging operations

Table 1 summarizes the results of the dredging operations carried out over a 5 year period from March, 1974, to March, 1979. The 40 dredge hauls listed in Table 1 are those where a sample of the bottom was recovered successfully. Many more hauls, over 60 in fact, were made where the dredge came up empty. The general location of each haul is given in Table 1 and Figure 1.

In the majority of the successful dredge hauls, sedimentary rock was recovered, but on most of the hauls made on the south wall of the Monterey Submarine Canyon only mud, clay, or gravel came up in the dredge. We made many other attempts to dredge rock from the canyon walls but collected no sample at all. This was a disappointment, for one of our objectives in this study was to sample the rocky wall of the canyon to determine if living stone borers were present and if they played a role in causing erosion and deepening of the canyon. In southern California, WARME, SCANLAND & MARSHALL (1971) found that Parapholas californica, Netastoma rostrata, Adula californiensis, and Lithophaga plumula bored intensely into the rocks of the rim and upper walls of the Scripps Submarine Canyon, and that in some areas these organisms were more important as eroders of rock than physical and chemical processes. Even though the walls of the Monterey Submarine Canyon are steep, it is apparent from our results that a sticky layer of clay covers most areas. Greene (1977) succeeded in recovering rock samples from both the north and south walls of the Monterey Canyon. In some cases these were granite samples, in others siltstone or sandstone. Many of the non-granitic rocks Greene recovered showed bore holes made by pholads and possibly mytilids, but no living borers were found. We must tentatively conclude, therefore, that living marine bivalve borers are not causing extensive erosion of the walls of the Monterey Canyon at the present time.

In the shallow subtidal water off Santa Cruz relatively few dredge hauls were successful in recovering samples. Off Capitola and Soquel Point a few successful hauls recovered samples from the Purisima Formation, and off the terraces to the west of Point Santa Cruz some samples of chert and mudstone were recovered. Most of these samples showed evidence of stone borer activity.

In the shallow water at the southern end of Monterey Bay, we were much more successful in recovering rock samples and living bivalve borers as is indicated in Table 1. In some cases the chain bag dredge would come up with one large block of chert that had been broken off a ledge, or a large flat concretion broken out of a cherty matrix. In other cases it picked up loose pieces of chert or rounded calcareous concretions that had been lying free on the bottom. Most samples collected off Del Monte Beach consisted of a mixture of these two rock types, and most samples showed extensive borer activity leading to considerable erosion of the rock.

We have collected two species of borer bivalves from subtidal shale off Del Monte Beach while diving, yet have never recovered either of them in dredged samples. Zirfaea pilsbryi is a larger pholad commonly found boring into stiff clay or hard mud at Elkhorn Slough. Off Del Monte Beach, it is relatively abundant, occupying vertical burrows in the softer shale and mudstone. The distinctive siphons made identification easy. This species is often found in densities of 5 animals per m². Zirfaea excavate burrows up to 60 cm deep in the shale that forms the flat bottom between elevated reefs. Dredging is therefore unlikely to recover rock samples containing Zirfaea. Diving observations have indicated that large animals of this species can project their siphons up through as much as 30 cm of sand cover.

A second species not collected by dredging, Barnea subtruncata, is somewhat smaller than Zirfaea. It too has distinctive siphons and lives in soft flat shale off Del Monte Beach but in numbers far fewer than Zirfaea.

Most of the boring bivalves found during this investigation had been collected earlier in Monterey Bay, and the subtidal shale off Del Monte Beach is the type locality for several species. One pholad, however, had never been collected before north of southern California (HADERLIE, 1979). Penitella fitchi was described from specimens collected from intertidal rock at Bahía San Bartolomé, Baja California (TURNER, 1955). Additional specimens have been found at Redondo Beach, La Jolla, and San Diego. Kennedy (1974) reported P. fitchi as a fossil in Pleistocene deposits from southern California and Baja California. During the present study, P. fitchi was found on four occasions. Single living animals were recovered on each of the dredge hauls numbers 20, 22 and 23. The animals were from 5.0 to 6.5 cm in shell length, were in the postboring stage, and occupied burrows in hard chert. On Dredge Haul No. 25, a single set of valves (4.0 cm long) of a dead specimen was found in a burrow in chert.

One of the objectives of the dredging part of this study was to determine the bathymetric distribution of boring bivalves in Monterey Bay. As will be pointed out below, some species occur in the intertidal zone at Santa Cruz as high as 2 m above MLLW (mean lower low water or zero tide level). Subtidally our dredging operations have shown (Table 1) that living bivalve borers are common down to depths of 50 m in the southern part of the Bay. Below a depth of 50 m very few living animals have been found in recovered rock samples, although many rocks brought up from these deeper waters were riddled with burrows that were identical to those made by living pholads in shallower water. Many of the bored rock samples from deeper water had been broken off by the dredge, so these samples had not been transported to deeper water.

Perhaps these bore holes were made by pholads in the past when the level of Monterey Bay was lower than at present, or when temperatures were different. The vacant holes do not appear to be geologically old, however, for they were not filled with compacted sediment and were often not even occupied by nestlers. Experiments now in progress (to be reported on later) have shown that very few boring bivalve larvae settle on or bore into experimental rock panels exposed in water depths exceeding 70 m in Monterey Bay.

3. INTERTIDAL REEFS NEAR SANTA CRUZ

One of the earliest reports on living bivalve borers in the intertidal zone at Santa Cruz was in the original edition of RICKETTS & CALVIN (1939). Ricketts had observed Platyodon cancellatus (Conrad, 1837) in enormous numbers in banks of stiff blue clay and noted their erosive influence along the shore. He also found siphons of Parapholas californica projecting from rocky reefs in the intertidal zone at Santa Cruz, but the exact location of the reefs was unspecified. In this investigation we have concentrated on the rocky reefs in the area to the west of Point Santa Cruz and have not observed large numbers of living Platyodon nor Parapholas. The few living Platyodon cancellatus observed appeared to be nestlers in vacated pholad burrows. In the blocks of Purisima Formation in the cliffs some 5 m above sea level at Santa Cruz, however, there are many Pliocene fossils of P. cancellatus to be seen as was reported by ADDICOTT (1966).

Most of the results of the investigation being reported on here from the intertidal zone at Santa Cruz were included in a thesis by CLARK (1978). This past year, studies have continued, particularly on the terraces west of Natural Bridges State Park.

On one large intertidal reef composed primarily of Monterey shale west of Point Santa Cruz, Clark found the following species of bivalve borers: Adula californiensis, A. falcata, Lithophaga plumula, Netastoma rostrata, Penitella gabbii, P. penita, and Parapholas californica. Of these, Penitella penita was by far the dominant species of borer and was found in rock ranging from the hardest chert to soft mudstone, from 0.7 to 2.0 m above MLLW, and in population densities of more than 10 mature individuals per 75 cm² surface area. Most individuals were found boring horizontally into ledges on the reef, particularly in pot holes where concretions had been displaced. Approximately half the P. penita were in the boring stage, half were mature with a fully-formed callum. The largest individuals had a shell length (exclusive of siphonoplax) of 5.7 cm.

The mytilid Adula californiensis was the second most common borer found on the reef at Santa Cruz. The largest of these had a shell length of 3 cm. All the other borers were present in much smaller numbers. Nestling bivalves occupying vacant pholad holes included Semele rupicola Dall, 1871, Hiatella arctica, Protothaca staminea Conrad, 1837, Petricola carditoides, Kellia laperousii and Platyodon cancellatus.

CLARK (1978) also studied the borers in a transect across a flat, gently sloping terrace of chert and mudstone located west of Natural Bridges State Park. He found that here, too, Penitella penita was the dominant borer with Adula californiensis, Penitella gabbii, and Netastoma rostrata present in smaller numbers. The highest level where any of these occurred was at 1.0m about MLLW where a few Penitella penita were found.

The broad terraces found between Natural Bridges State Park and Terrace Point are broken periodically by wide channels which cut through the terraces all the way up to the base of the sea cliff some 40 m shoreward from low water level. These channels have a floor of sand which varies in thickness throughout the year. Where these channels have cut through the terraces they have left vertical walls on each side, some 2 m or more high in some places. During this past year these exposed vertical sections of the terraces have been examined for stone borers. Shifting sand along the lower part of these walls erodes the rock very fast and many of the vertical walls are severely undercut. These regions harbor relatively few stone borers, mainly Penitella penita and Netastoma rostrata, and all individuals recovered were small and immature. It is possible that borers cannot survive long enough to reach maturity in this substrate being rapidly abraded by moving sand. In the vertical walls above the area of major sand movement, however, many Penitella borers were found and about half of these were large mature animals. Penitella penita again was the dominant species observed, but P. gabbii was also common. Netastoma rostrata and Adula californiensis were also present, but in small numbers. Chaceia ovoidea was also found boring horizontally into these intertidal rock walls. Firch (1953) reported Chaceia as being common at Santa Cruz, but CLARK (1978) did not observe this species during his work on the intertidal reefs and terraces. During this past year many specimens of C. ovoidea have been collected from the walls of the surge channels near Terrace Point at levels of 0.5 to 1.0 m above MLLW. All of the Chaceia so far observed have been small, up to 1.7 cm shell length, and in the immature boring stage, and no large Chaceia burrows have been seen, as are common in subtidal waters off Monterey. This would indicate that even the upper walls of

the surge channels through these intertidal terraces erode away and expose the *Chaceia* before these long-lived borers become mature.

4. Carbonate and petrographic analyses of rock samples

The literature on rock boring organisms extends back for more than 200 years. Yet, many of the problems considered in these published studies and observations remain unresolved. At times in the past it has been fashionable to divide stone borers into two large categories, those that appear to dissolve the rock by chemical means, and those that abrade the rock mechanically. Among the bivalve borers, the mytilids, such as Lithophaga and Adula, have been considered chemical borers despite the fact there is no direct evidence to support the contention. Pholads as a whole have been considered to be mechanical borers, a conclusion based primarily on the functional morphology of these animals and their shells. The investigation being reported on here from Monterey Bay does not answer any of the lingering questions regarding the specific method or methods used by bivalves in burrowing into solid rock substrates. These studies have shown, however, that methods used for boring may be far more complex than we have suspected, and any one borer may be able to use a variety of methods for excavating burrows into various rocks having different physical and chemical properties. The fact that Lithophaga plumula (usually considered to be a chemical borer living primarily in calcium carbonate substrates) and various species of the genus Penitella (usually considered to be mechanical borers living primarily in soft rock) can live side by side and reach maximum size while boring into exceedingly hard, dense, siliceous chert in the shallow subtidal and intertidal zone of Monterey Bay indicates that we have much to learn about the fundamental mechanisms of rock boring in marine animals.

The dominant rock types where living bivalve borers have been found in the present investigation in Monterey Bay fall into three main categories: (1) silty biogenic cherts and siliceous shales of the Monterey Formation, (2) calcareous concretions of various shapes and sizes associated with the chert beds or derived from them and lying free on the bottom, and (3) Purisima Formation dredged from shallow water at the north end of the Bay. We have attempted to learn something about the physical and chemical nature of the first two types of these rocks into which many species of bivalves so regularly erode sizable burrows.

The amount of CaCO3 in any of the samples from the Monterey Formation (except for concretions), be they relatively soft mudstone or exceedingly hard chert, was extremely low, varying from 0.03 percent in some samples to a maximum of 0.74 percent in others. Analysis of thin sections of chert from the Santa Cruz reef and from subtidal outcrops off Del Monte Beach showed it to be primarily (90 - 95%) a ground mass of siliceous biogenic hash (radiolaria, sponge spicules, diatoms, etc.) with 5-8 percent clasts of silt-sized quartz, feldspar, biotite, magnetite, hematite, and microcrystalline chert. No cementation was present.

Chemical analysis of the concretions, both from the subtidal waters in Monterey Bay and from the reefs in the intertidal zone at Santa Cruz, gave a CaCO3 content of 80-85 percent. Thin sections demonstrated that the concretions were recrystallized fossiliferous limestone with a ground mass of muddy carbonate now recrystallized to sparry calcite. The fossils were recrystallized foraminifera and siliceous tests replaced by calcite.

SUMMARY

- This paper presents the results of a 10 year study on the distribution of bivalve mollusks that bore into rocky substrates in Monterey Bay.
- 2. Living borers were found in all types of sedimentary rocks from 2 m above MLLW to depths of over 50 m.
- 3. The Monterey shale exposed under the kelp beds in southern Monterey Bay has been examined by divers and 11 species of bivalve borers have been identified including the mytilids Adula falcata, A. californiensis, Lithophaga plumula, and the pholads Barnea subtruncata, Chaceia ovoidea, Netastoma rostrata, Parapholas californica, Penitella conradi, P. gabbii, P. penita, and Zirfaea pilsbryi.
- 4. Over 100 dredge hauls were made at various places in Monterey Bay from the shallow water off Santa Cruz to deep water in the Monterey Canyon. Forty of these hauls were successful in recovering a bottom sample. In water down to 50 m deep in the southern part of the Bay, rock samples recovered carried the same borers as were found in the diving operations, with the exceptions of Adula californiensis, Barnea subtruncata, and Zirfaea pilsbryi. In addition, the dredging recovered a species not previously reported from Monterey Bay, Penitella fitchi. Dredging in shallow water off Santa Cruz recovered samples of Purisima Formation with a variety of borers.

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- 5. In deeper water of Monterey Bay, recovered rock samples showed evidence of bivalve borer activity, but no living borers were found.
- 6. Few samples of sedimentary rock were recovered from the walls of the Monterey Canyon and none carried living borers.
- The intertidal reefs at Santa Cruz were populated, from low tide level to 2 m above MLLW, with Adula californiensis, A. falcata, Lithophaga plumula, Chaceia ovoidea, Netastoma rostrata, Parapholas californica, Penitella gabbii and P. penita. Of these, Penitella penita was the dominant species.
- 8. Chemical and petrographic analyses of various rock samples indicated that most of the bivalve borers in Monterey Bay bore into both siliceous rocks of various hardness and into calcareous rocks.

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